

Rainfall effects on rare annual plants

Jonathan M. Levine^{1*}, A. Kathryn McEachern² and Clark Cowan¹

¹Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA; and

²USGS-BRD-WERC, Channel Islands Field Station, 1901 Spinnaker Dr., Ventura, CA 93001, USA

Summary

1. Variation in climate is predicted to increase over much of the planet this century. Forecasting species persistence with climate change thus requires understanding of how populations respond to climate variability, and the mechanisms underlying this response. Variable rainfall is well known to drive fluctuations in annual plant populations, yet the degree to which population response is driven by between-year variation in germination cueing, water limitation or competitive suppression is poorly understood.

2. We used demographic monitoring and population models to examine how three seed banking, rare annual plants of the California Channel Islands respond to natural variation in precipitation and their competitive environments. Island plants are particularly threatened by climate change because their current ranges are unlikely to overlap regions that are climatically favourable in the future.

3. Species showed 9 to 100-fold between-year variation in plant density over the 5–12 years of censusing, including a severe drought and a wet El Niño year. During the drought, population sizes were low for all species. However, even in non-drought years, population sizes and per capita growth rates showed considerable temporal variation, variation that was uncorrelated with total rainfall. These population fluctuations were instead correlated with the temperature after the first major storm event of the season, a germination cue for annual plants.

4. Temporal variation in the density of the focal species was uncorrelated with the total vegetative cover in the surrounding community, suggesting that variation in competitive environments does not strongly determine population fluctuations. At the same time, the uncorrelated responses of the focal species and their competitors to environmental variation may favour persistence via the storage effect.

5. Population growth rate analyses suggested differential endangerment of the focal annuals. Elasticity analyses and life table response experiments indicated that variation in germination has the same potential as the seeds produced per germinant to drive variation in population growth rates, but only the former was clearly related to rainfall.

6. *Synthesis.* Our work suggests that future changes in the timing and temperatures associated with the first major rains, acting through germination, may more strongly affect population persistence than changes in season-long rainfall.

Key-words: annual plant population, climate variability, germination, persistence, precipitation

Introduction

Increasing evidence for global climate change has motivated ecologists to examine how forecasted changes in environmental variables will influence natural communities. Much of this work has focused on changes in mean conditions, such as temperature and precipitation (Root *et al.* 2003; Thomas *et al.* 2004). Far less explored are the potential impacts of

forecasted changes in variation around those means (Knapp *et al.* 2002; Karl & Trenberth 2003; Salinger 2005; Adler *et al.* 2006).

Ecological theory predicts both negative and positive effects of increasing environmental variability on species persistence. Increasing variance in vital rates tends to decrease long-term average population growth rates (Lande 1988; Tuljapurkar 1990; Boyce 1992; Higgins *et al.* 2000; Menges 2000). Environmental variation can also threaten populations when extreme years are catastrophic. Alternatively,

*Correspondence author. E-mail: levine@lifesci.ucsb.edu

temporal environmental variation can benefit species persistence through the storage effect (Chesson 2000; Levine & Rees 2004; Adler *et al.* 2006). If species differ in the years in which they experience their maximal performance, climatic fluctuations enable rare species to avoid interspecific competition. Forecasting species persistence in a changing climate thus requires understanding of how populations respond to climate variability and the mechanisms underlying this response (Fieberg & Ellner 2001; Meyer *et al.* 2006).

On an annual basis, precipitation is among the most temporally variable climate factors, and in many regions of North America, rainfall is forecast to become even more variable over the next century (Bell *et al.* 2004; Salinger 2005). Variable precipitation is known to drive particularly large variation in the populations of annual plants (Talbot *et al.* 1939; Went 1948; Heady 1958; Beatley 1974; Young *et al.* 1981; Gutierrez & Meserve 2003; Fox *et al.* 2006; Angert *et al.* 2007). Nonetheless, the specific mechanisms by which rainfall influences plant demographics are more complicated than commonly believed, involving at least three hypothesized mechanisms.

The most intuitive mechanism, and the one commonly assumed to operate, is water limitation. In arid systems, where water is known to be a limiting factor, wet years may ease water limitation of vital rates such as survival and fecundity, whereas dry years may not even provide the water resources necessary for successful completion of the life cycle (Gutierrez & Meserve 2003; Adler & Levine 2007).

A second mechanism by which rainfall drives fluctuations in annual plant populations is between-year variation in germination cueing. Rainfall years differ greatly in the timing and conditions coincident with the germination-inducing storm, cues that regulate germination and the size of the emergent population (Went 1948; Beatley 1974; Baskin & Baskin 2001). This mechanism is related to the first in that selection should favour germination in response to environmental cues predictive of future moisture conditions (Pake & Venable 1996). Indeed, winter desert annuals germinate best when the temperature at the time of seed wetting is cool (Went 1948; Beatley 1974), presumably indicative of upcoming winter rains. In fact, if temperature conditions required for germination are not met by early storms, subsequent precipitation may have little effect on desert annual population dynamics (Beatley 1974). More general appreciation for the possibility that variation in germination cueing underlies plant population fluctuations is only beginning to develop.

While the first two mechanisms involve direct responses to rainfall conditions, a third mechanism poses that plant populations may fluctuate with climate due to indirect effects mediated by changes in the surrounding community (Levine & Rees 2004). If rainfall variability drives large between-year variation in the competitive environment of a focal species, its population may fluctuate because of temporal variation in competitive suppression. For example, Pitt & Heady (1978) argue that mid-winter drought years favour the deep rooted *Erodium* in California grasslands because such years are disproportionately stressful for their exotic grass competitors.

Varying rainfall can thus influence annual plant population dynamics through 'water limitation', 'germination cueing', and 'competitive suppression' mechanisms, or some combination of the three. Determining when each process dominates is critical to forecasting how populations will respond to the wetter or drier climates of the future, or the warmer temperatures that will presumably accompany the germination-inducing rains. Evaluating these mechanisms is also important for predicting beneficial effects of environmental variability on persistence. If population variability is controlled largely by germination cueing, and competitors differ in their cues, environmental variation can strongly buffer species from extinction via the storage effect (Chesson 1990, 2000; Pake & Venable 1996). Similar buffering arises from differential effects of water limitation on different species.

An understanding of the mechanisms underlying fluctuations in annual plant populations is incomplete without seed bank dynamics. Most evidence for extreme variability in annual plant systems comes from the germinated fraction of the population (Talbot *et al.* 1939; Heady *et al.* 1958; Bowers 1987; but see Pake & Venable 1996; Gutierrez & Meserve 2003). Yet, this may translate only weakly into effects on population growth rates (Doak *et al.* 2002). Numerous models have shown how seed banks buffer population dynamics through large fluctuations in the performance of germinated individuals (Cohen 1966; Ellner 1985; Rees & Long 1992). Nonetheless, these models have rarely been parameterized with field data (Menges 2000; Doak *et al.* 2002; Meyer *et al.* 2006), and thus we have little understanding of the true variability in annual plant population growth and the factors controlling this variability.

In this study we examine how the populations of three seed banking, rare annual plants endemic to the California Channel Islands respond to wide variation in precipitation and the mechanisms underlying their response. Island endemic plants such as these are particularly threatened by climate change because their current ranges are unlikely to overlap regions that are climatically favourable in the future (Walther *et al.* 2002; Thomas *et al.* 2004) and their often small populations make them particularly sensitive to climatic variability. Moreover, restricted dispersal prevents them from reaching more favourable habitats in the future, and thus their persistence depends on how they respond to climate change in their current locations.

To evaluate the different mechanisms underlying plant population response to climate, we monitored the emergent populations of three different annuals and their competitors over 5–12 years, a period including severe drought and wet El Niño years (Schonher & Nicholson 1989; McPhaden *et al.* 2006). We then correlated emergent population size with variables related to germination, water limitation and competition. To examine between-year variation in population growth rates, we combined the monitoring data with vital rates obtained in experimentally sown plots. We then used elasticity analyses and life table response experiments (Caswell 2001) to evaluate the mechanisms responsible for

temporal variation in population growth rates. Lastly, we used the demographic data to assess the relative endangerment of our three focal species, and the type of climate years most critical to population persistence.

Methods

STUDY SYSTEM

All field work was conducted on Santa Rosa Island, roughly 40 km off the coast of Santa Barbara and under the jurisdiction of the National Park Service. The climate is Mediterranean with cool, wet winters and warm dry summers. We obtained precipitation data from a weather station deployed on Santa Rosa Island since 1990 (Fig. 1a). Precipitation over the last 17 years averages 32 cm, and varies sixfold over this time period. The current study examined populations from 2002 to 2007, with *Gilia* population censuses extending back to 1994. Although our work concentrates on 2002–07, this period included the wet 2004–05 El Niño event, and the severe 2006–07 drought year. Moreover, these years covered large variation in the temperature at the time of the first major rains. Hereafter, we will refer to rainfall years by the year of the spring, so the El Niño year will be ‘2005’ and the drought year ‘2007’.

Our study examined the dynamics of three rare and endangered annual plants, *Gilia tenuiflora* ssp. *hoffmannii*, *Malacothrix indecora* and *Phacelia insularis* var. *insularis* (hereafter *Gilia*, *Malacothrix* and *Phacelia*) on Santa Rosa Island (Thomas 2000). *Gilia* is found on stabilized dune soils, co-occurring with other annual plants. *Malacothrix* is found on sandy, eroding terraces dominated by the native annual grass *Lasthenia californica*, and several perennial grass species. *Phacelia* is found on stabilized dune headlands, and occurs in small clearings within an otherwise dense cover of the exotic annual grass, *Bromus diandrus*. All three focal species are endemic to the northern Channel Islands, and federally listed as endangered. All germinate with the first major (> 2.5 cm) rains of the fall or winter, develop a taproot, and are small statured. Flowering peaks in early March, mid-April and early June for *Phacelia*, *Gilia* and *Malacothrix*, respectively.

QUANTIFYING NATURAL POPULATION DYNAMICS

Against natural variation in precipitation we monitored the population size and fecundity of the focal annuals at peak flowering each spring from 2003 to 2007. We also followed the dynamics of the community surrounding our three focal species through estimates of vegetative cover. The sampling design varied with the spatial dispersion and abundance of the different species, and only included the above-ground component of the populations. Because sampling natural germinants is difficult due to their small size and broad distribution, we quantified early life stage and seed bank dynamics in sown plots as discussed in the next section.

For *Gilia*, we counted all individuals in one-hundred 1 m² circular plots, in a stratified random design encompassing five adjacent 60-m wide, 100-m long elevational bands. In half of the plots, we recorded flower number for three randomly located plants, and took the average value for analysis. One of us (AKM) had been censusing the *Gilia* population since 1994 with this method, and thus we present census results dating back to this year. For *Malacothrix*, we censused all individuals in seven large (40–100 m²) plots. We counted flower number on 15 randomly located individuals per plot, which were averaged within plot before analysis. For *Phacelia*, the

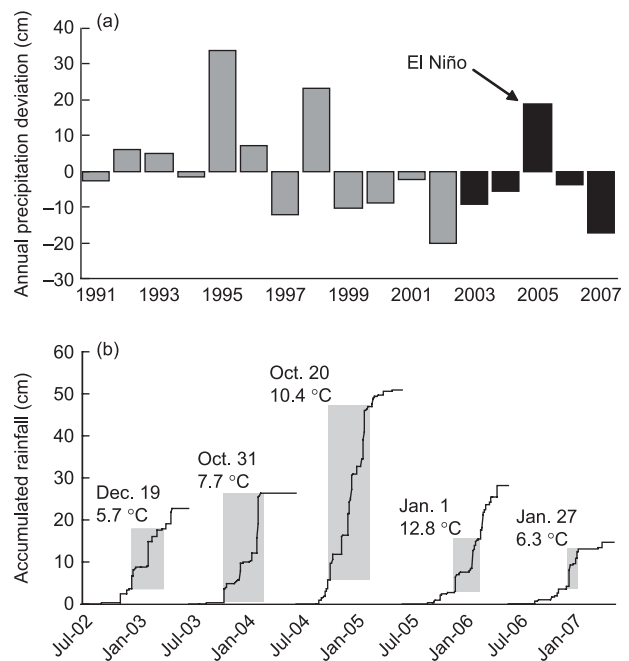


Fig. 1. (a) Annual precipitation deviation from the 17-year mean (32 cm) on Santa Rosa Island from 1990 to 2007. Black bars show the focal period of the current study. (b) Accumulated precipitation in the five rainfall seasons examined. The grey boxes delineate the period from the first major rains (germination) through the first week of March – the period of peak flowering for *Phacelia insularis* var. *insularis* and the onset of flowering for *Gilia tenuiflora* ssp. *hoffmannii*. The date of the first rains (> 2.5 cm) and the 5-day average low temperature thereafter are indicated in the upper corner of each box.

most sparse of our species, we censused all individuals in four large sampling plots (up to 500 m²). At three of four sites, we counted flower number in ten 0.25 m² circular plots centred on flagged individuals from the census.

ESTIMATING POPULATION GROWTH RATES

We parameterized an annual plant population model to estimate per capita population growth rates under the varying precipitation regimes in 2004, 2005 and 2006. Mathematical models describing the dynamics of annual plant populations are well-developed (Watkinson 1980; Pacala 1986; Levine & Rees 2004) and provide a reasonable approximation of the annual life cycle. Importantly, they do not require direct estimates of seed bank size, only the seed mortality rate in the soil. Population growth from one year to the next (λ), including both above- and below-ground processes, can be described as follows:

$$\lambda = s(1 - g) + gF \quad \text{eqn 1}$$

g is the fraction of germinating seeds, s is the annual survival of ungerminated seeds in the soil, and F is the number of viable seeds produced per germinant. The first part of the sum is the per seed contribution to growth through seed bank carryover – the fraction that do not germinate but survive. The second part is per seed production of new seeds through germination and seed production.

An important assumption of the model is that annual seed survival and germination rates do not change with seed age. A second assumption is that no seeds leave the population, an assumption

very likely violated for *Malacothrix* and *Phacelia*, in particular. These species live in small patches of suitable habitat, and as a consequence, disperse some of their seeds to unsuitable locations. Thus, the population growth rates we calculate are upper bounds for the true growth rates. Even so, these rates are useful for comparing growth across years.

ESTIMATING MODEL PARAMETERS

The natural population census provides information on only part of the annual plant life cycle necessary for model parameterization, namely the flowers produced per surviving individual. We measured germination fractions, plant survival, and seed bank survival with experimentally seeded plots and buried bags of seed. To estimate the germination rate each year, and the survival of those germinants to the end of the growing season, we seeded plots with a known numbers of seeds in the 2004, 2005 and 2006 seasons. Each year, these plots were randomly located along transects in areas nearby but not in our study populations. Each plot included a cleared and uncleared subplot of 15 × 15 cm, covering the range of heterospecific density in the surrounding community. *Phacelia* and *Gilia* germinated so few seeds and/or responded so weakly to vegetation clearing, that we pooled the two subplots for analysis. Although 2004 *Malacothrix* survival was higher in cleared subplots, we pooled demographics from *Malacothrix* subplots for consistency with the two other species. Sample size varies among species and years (ranging from $n = 8$ to $n = 27$) because the plots were the controls for other experiments.

In the fall of each year, we seeded the three focal species into plots at each of their island locations. The amount of seed sown varied across year and species due to seed availability in the field the previous spring. Thus in the 2004, 2005 and 2006 seasons, we sowed the plots with 40, 80 and 120 seeds, respectively, of *Phacelia*; 200, 100 and 260 seeds, respectively, of *Malacothrix* and 200, 400 and 400 seeds, respectively, of *Gilia*. Germination rates and plant size were low enough in all years that interaction among the seeded individuals was minimal. Except for the first year, when *Phacelia* was relatively abundant, we used *Phacelia* seed collected from plants reared in the greenhouse or experimental field plots.

In each plot, we measured germination by placing a toothpick near each plant observed in multiple censuses beginning after the first major rains. The number of germinants was divided by the total number of seeds added, discounted by their viability to estimate the germination rate. Plant survival was the fraction of the germinants present at the flowering period. To estimate the seeds produced per germinant, F , we used the product of survivorship from the seeded plots, flower number per (surviving) plant from the natural populations, and seeds per flower and viability from a sample of natural plants. We did not measure the number of seeds per flower each year. Thus, for all years we used a common value obtained from plants collected in 2006 for *Gilia* and *Malacothrix* (23.2 ± 1.5 and 28.3 ± 2.6 , respectively) and 2005 for *Phacelia* (8.0 ± 2.5).

We estimated seed survival in the soil by burying polyester mesh bags of 50 (*Malacothrix* and *Phacelia*) and 100 seeds (*Gilia*) in November, and retrieving the bags 1 year later. Burial occurred in 2003 for *Gilia* and *Malacothrix*, and 2004 for *Phacelia*. Seed viability before and after 1 year of burial was assessed by germinating seeds on wetted germination paper at 5 °C for 5 days and then 20 °C for 2 weeks thereafter. Those that did not germinate were cut, treated with gibberellic acid, and then stained with tetrazolium to check viability. Because of the time consuming nature of these tasks, we made the assumption that seed survival was constant with seed age, and did not differ between years. Elasticity analyses described in the

next section help us evaluate how variation in seed survival and seeds per flower would influence population growth rates.

ELASTICITY ANALYSES AND LIFE TABLE RESPONSE EXPERIMENTS

Considering that the germination cueing and water limitation mechanisms invoke different life history transitions to explain variation in population growth rate, we evaluated the degree to which variation in germination vs. the performance of germinated individuals influences population growth rates. Specifically, we calculated the elasticity of λ to g , $((g/\lambda) (\partial\lambda/\partial g))$, F , $((F/\lambda) (\partial\lambda/\partial F))$, and s , $((s/\lambda) (\partial\lambda/\partial s))$, in all 3 years. These elasticities describe how a proportional change in each demographic parameter influences the population growth rate.

We next conducted life table response experiments to evaluate the degree to which variation in population growth rate across years is driven by observed variation in g or F (Caswell 2001). Specifically we assume that the difference between the population growth rate in a given year and the average population growth rate across years ($\bar{\lambda}$) is a linear combination of the effects of changing g and F :

$$\lambda^{\text{year}} = \bar{\lambda} + (g^{\text{year}} - \bar{g}) \frac{\partial\lambda}{\partial g} + (F^{\text{year}} - \bar{F}) \frac{\partial\lambda}{\partial F} \quad \text{eqn 2}$$

The partial derivatives are evaluated at \bar{g} and \bar{F} (the 3-year average for these parameters), and the *year* superscript indicates 2004, 2005 or 2006. Equation 2 allows us to project how the per capita growth rate would change across years if only the germination rate varied ($F^{\text{year}} - \bar{F} = 0$) or only the seeds produced per germinant (F) varied ($g^{\text{year}} - \bar{g} = 0$). By comparing these two projections to the observed variation in per capita growth rate, we can assess the contributions of the observed variation in each parameter to variation in λ . Because the seed death rate, s , is assumed to be constant across years ($s^{\text{year}} - \bar{s} = 0$) and thus does not contribute to temporal variation in λ , it is absent from eqn 2.

Results

RAINFALL PATTERNS

Of the five focal years of our study, the first 2 years (2003, 2004) covered near average rainfall years, while the 2005 El Niño event brought over 50% more rain than the 17-year average (Fig. 1). Importantly, 92% of this rain fell by the first week of March, the period prior to peak flowering for *Phacelia*, and the onset of flowering for *Gilia*. In fact, total precipitation by the first week of March was the highest in the 17 years recorded by the weather station. Ultimately, the 1995 and 1998 rainfall years had higher season-long totals than 2005, but this was due to more rain later in the season. By contrast, < 15 cm of rain fell in 2007 – less than half the 17-year average. This included a germination-inducing storm in late January, and only one large (> 2 cm) subsequent rain event.

Years also differed markedly in the timing and air temperature associated with the first major storm (by ‘major’, we mean a storm over 2.5 cm – an amount required for the germination of California annuals (Heady *et al.* 1958; Beatley 1974; Bartolome 1979). Every year had such a storm, but over the 5 years of censusing, its date varied by over 3 months and

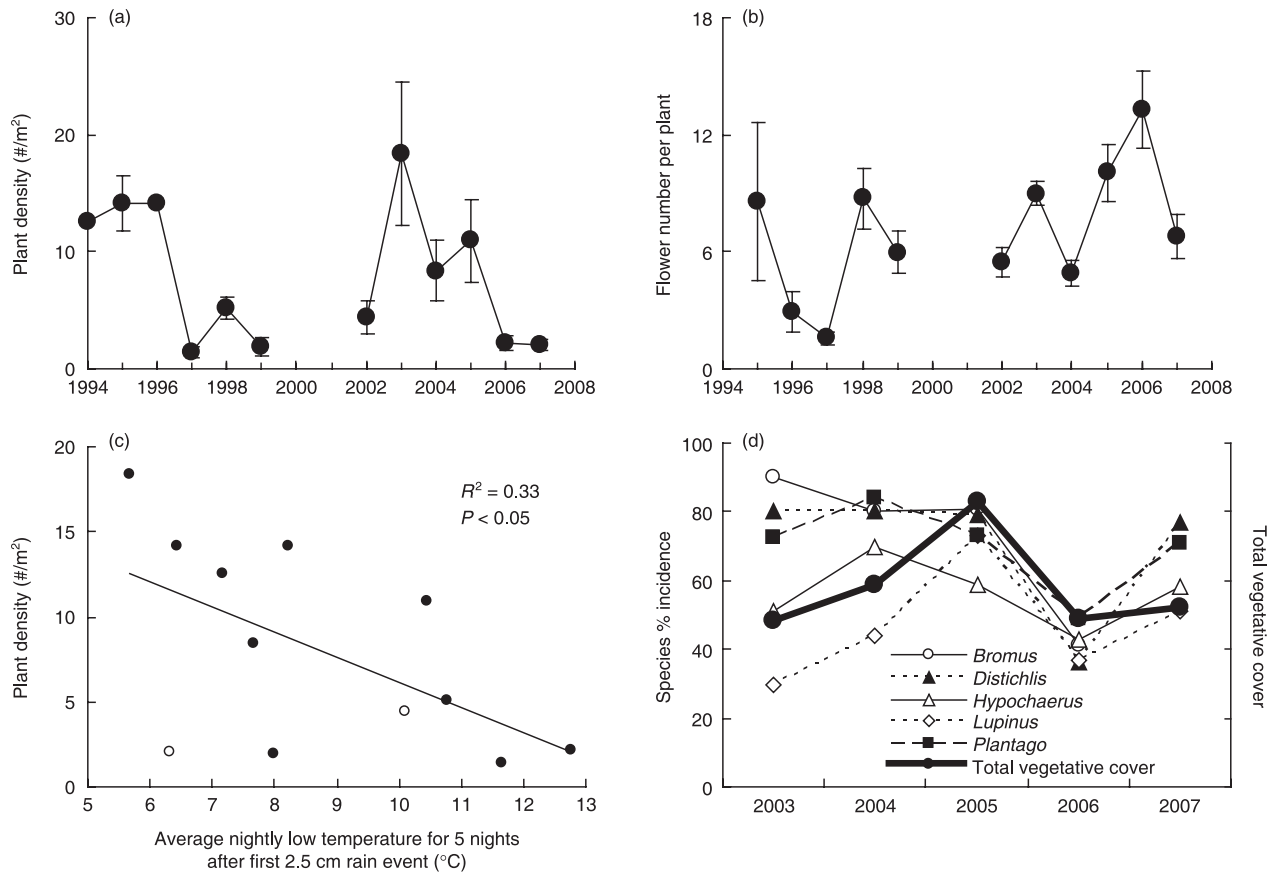


Fig. 2. Fluctuations in the (a) springtime plant density and (b) flower number of *Gilia tenuiflora* ssp. *hoffmannii*. Points show means \pm 1 SE. (c) Relationship between *Gilia* plant density and the average low temperature after the first major rains of the year. Open circles show the two severe drought years of 2002 and 2007. When these points are removed, and only non-drought years examined, the temperature at the time of the first major rains explains 58% of the plant density variation ($P = 0.01$). (d) Fluctuations in the total vegetative cover of the surrounding community, and the proportion of plots in which the five most common species were found across the 5 year time series.

the 5-day average low temperatures after this storm varied by 7 °C (Fig. 1b). The relatively warm first rains happened to occur in the El Niño (2005) and La Niña (2006) years.

TEMPORAL VARIATION IN SPRINGTIME PLANT DENSITY

Against this natural variation in rainfall across years, all three species showed large between-year variation in the size of the emergent plant populations at the end of the growing season. *Gilia* exhibited ninefold variation in plant density in spring across the five focal years of our study, and a similar range of density is seen going back to 1994 (Fig. 2a). As expected with the water limitation mechanism, *Gilia* plants were relatively sparse during the 2002 and 2007 drought years. Equally striking, however, was the large between-year variation in plant density outside of the drought years, variation that seemed unrelated to total rainfall. Plant density was only marginally above average in the wet 2005 El Niño year and below average in the even wetter 1998 El Niño year. Meanwhile, in 2006, a year with near average rainfall, density was as low as in the 2007 drought. The number of flowers per plant was similarly variable across years and seemingly unrelated to total annual

rainfall (Fig. 2b). Indeed, there was no significant correlation between total annual precipitation and *Gilia* density ($R^2 = 0.19$, $P = 0.16$) or flower number ($R^2 = 0.11$, $P = 0.31$) across the 12-year data set.

By contrast, 33% of the variation in *Gilia* density was explained by the average nightly low temperature after the first major rains ($P < 0.05$, Fig. 2c), a variable long thought important for the germination of California winter annuals (Went 1949; Baskin & Baskin 2001). Moreover, the fraction of explained variation increases to 58% when the two severe drought years (open circles), are removed from the analysis. In sum, although *Gilia* plant density is low in drought years, the population is still highly variable in non-drought years. Most of this variation is explained by the temperature at the time of the first major rains, a germination cue.

Over the 5 years community data were collected, total vegetative cover in the *Gilia* habitat ranged from 50–80%, with the highest value obtained in the 2005 El Niño year (Fig. 2). However, temporal variation in *Gilia* density was uncorrelated with total vegetative cover ($R^2 = 0.026$, $P = 0.796$), suggesting that variation in competitive environments among years does not strongly determine *Gilia* density. However, the differential responses of *Gilia* and its competitors to

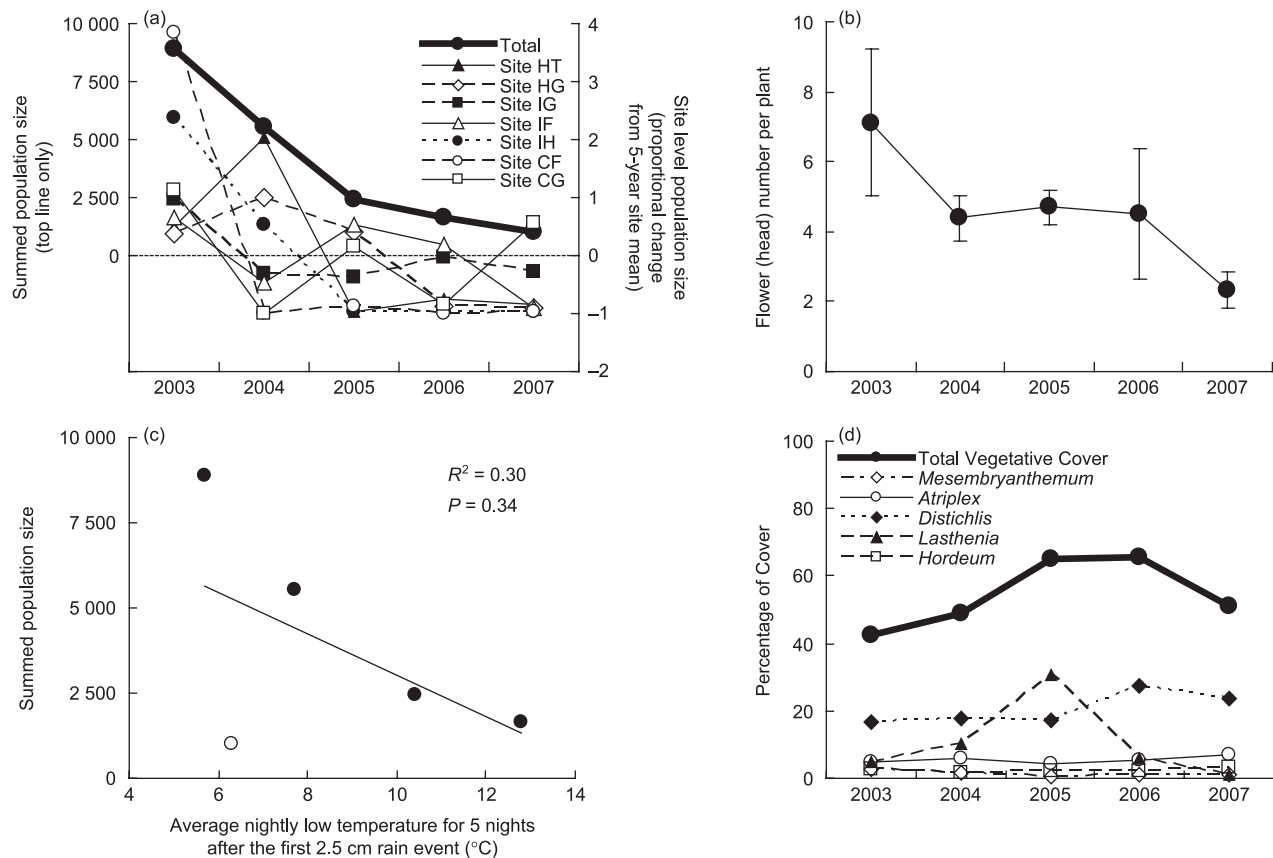


Fig. 3. Fluctuations in the (a) springtime plant population size and (b) flower number of *Malacothrix indecora*. Points show means ± 1 SE. In (a), the second y-axis shows the deviation of each site's population from its 5-year mean, divided through by that mean. (c) Relationship between *Malacothrix* springtime plant population size and the average low temperature after the first major rains of the year. The open circle shows the severe drought year of 2007. When this point is removed, and only non-drought years examined, the temperature at the time of the first major rains explains 93% of the population variation ($P = 0.04$). (d) Fluctuations in the total vegetative cover of the surrounding community and the cover of the five most common species.

environmental variation may favour *Gilia* persistence via the storage effect.

Plant abundance results for *Malacothrix* and *Phacelia* showed very similar patterns, though we have a shorter time series over which to evaluate population fluctuations. Springtime abundance of *Malacothrix* plants summed across the seven sites varied ninefold over the 5 years of study (Fig. 3a). As with *Gilia*, the 2007 drought year led to low plant abundance, though considerable variation remained in non-drought years. The greatest number of plants was observed in the more average rainfall years of 2003 and 2004. Sites varied in their response to the different rainfall years, though at none of these sites were populations largest or most fecund during the wet year of 2005 (Fig. 3a,b). Although correlations with climatic variables over only 5 years are necessarily uncertain, about one-third of the variation in *Malacothrix* abundance, like that of *Gilia*, was explained by the temperature at the time of the first major rains (Fig. 3c). This correlation was non-significant due to low sample size, but excluding the 2007 drought year leaves 93% of the variation in *Malacothrix* density explained by the temperature at the time of the first rains ($P = 0.04$). Dynamics of the surrounding community (Fig. 3d) may also play some role in driving *Malacothrix*

dynamics as its abundance was negatively, but not significantly correlated with the total vegetative cover of the surrounding community ($R^2 = 0.536$, $P = 0.160$).

Of the three focal species, *Phacelia* showed the greatest between-year variation in springtime plant abundance, ranging 100-fold. Again, population sizes were low during the 2007 drought year, and considerably variable in non-drought years. In a pattern very similar to *Malacothrix*, the greatest number of plants was observed in the more average rainfall years of 2003 and 2004 (Fig. 4b), potentially related to the colder first rains of these years. Plants were barely present in the 2005 El Niño and 2006 La Niña years, though it was these years in which plant fecundity was highest (Fig. 4a). Changes in *Phacelia* density through time were highly similar across three of the four sites (Fig. 4b). Although we have only 5 years of *Phacelia* censusing, 40% of the between-year variation in its abundance was explained by the temperature at the time of the first major rains (Fig. 4c). As with *Gilia* and *Malacothrix*, a much higher fraction of the variation is explained when only non-drought years are examined, and the correlation becomes significant ($R^2 = 0.92$, $P = 0.04$). Lastly, *Phacelia* density was not correlated with the total cover in the surrounding community (Fig. 4d, $R^2 = 0.001$, $P = 0.959$). As with

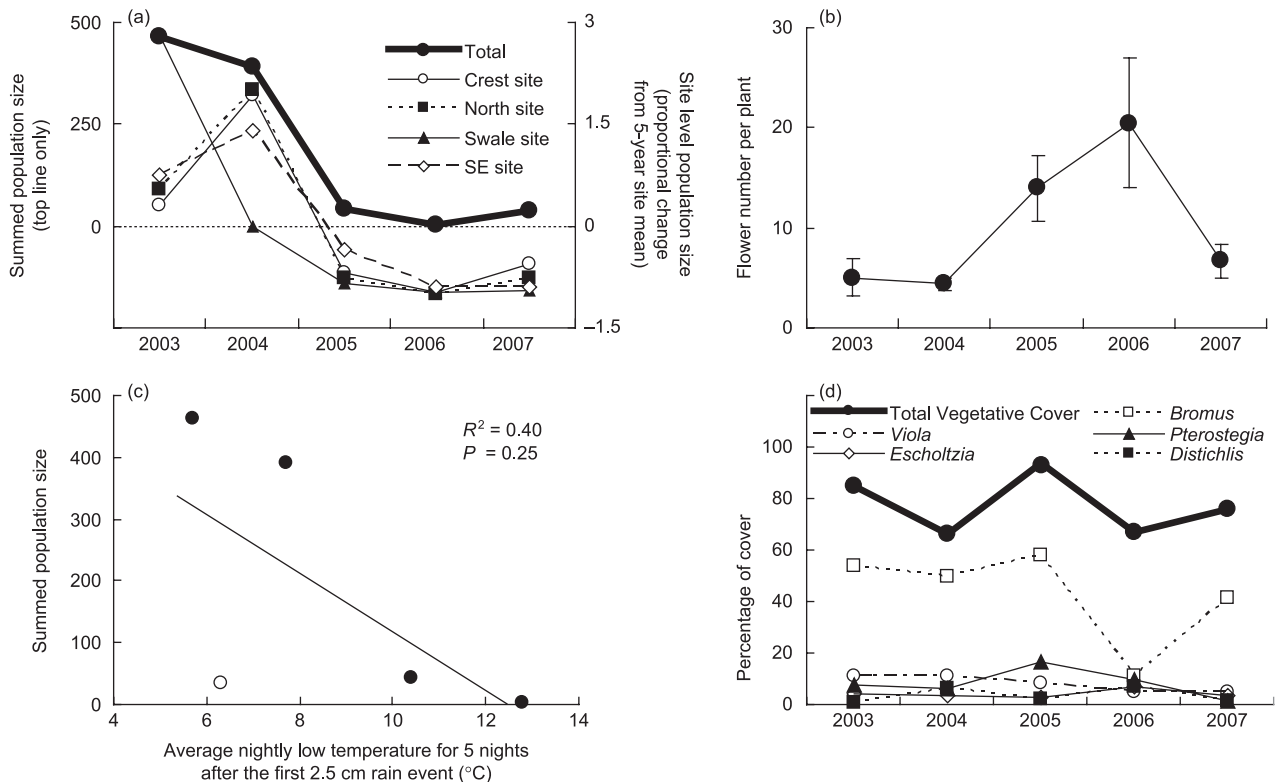


Fig. 4. Fluctuations in the (a) springtime plant population size and (b) flower number of *Phacelia insularis* var. *insularis*. Points show means ± 1 SE. In (a), the second y-axis shows the deviation of each site's population from its 5-year mean, divided through by that mean. (c) Relationship between *Phacelia* springtime plant population size and the average low temperature after the first major rains of the year. The open circle shows the severe drought year of 2007. When this point is removed, and only non-drought years examined, the temperature at the time of the first major rains explains 92% of the population variation ($P = 0.04$). (d) Fluctuations in the total vegetative cover of the surrounding community and the cover of the five most common species.

similar results for *Gilia*, this suggests that temporal variation in competition is not the major driver of *Phacelia* dynamics, and that the storage effect may favour its persistence.

DEMOGRAPHIC RESPONSE TO DIFFERENT RAINFALL YEARS

Among-year variation in population growth rates estimated for the non-drought years of 2004–06 (Fig. 5g–i) provided weak support for the water limitation mechanism. In fact, *Gilia* and *Malacothrix* had their lowest estimated population growth rates during the wet 2005 El Niño year, while *Phacelia* had negative population growth in this year. The low 2005 growth rate for *Gilia* corresponded to low germination (Fig. 5a), while for *Malacothrix* it corresponded to low seeds produced per germinant (Fig. 5e). These growth rates incorporated seed viability rates for *Gilia*, *Malacothrix* and *Phacelia* at 98%, 84% and 90%, and annual seed survival of 75%, 57% and 57%, respectively. Overall, the demographic data provided better support for the germination cueing mechanism. *Gilia* and *Phacelia* germination were highest in 2004 (Fig. 5), when temperatures were coolest immediately after the first storm (Fig. 1b).

Elasticity analyses show that regardless of their cause, proportional changes in the germination rate and the

performance of germinated individuals should have comparable effects on the population growth rates of the three focal species (Table 1). Given that no single demographic variable most strongly controls population growth (Table 1), any of our three mechanisms could regulate temporal variation in population growth rates.

That the elasticities of λ to germination and seeds produced per germinant would be highly similar could be predicted analytically. With annual plant dynamics described by eqn 1, the elasticity of λ to germination is $g(F - s)/\lambda$ while the elasticity of λ to seeds produced per germinant is gF/λ . As long as the seeds produced per germinant (F) is much greater than the seed survival in the soil (s), these two elasticities are roughly equivalent.

Consistent with the elasticity analyses, life table response experiments showed that between-year variation in both germination and the seeds produced per germinant underlie the temporal variation in λ . Figure 6a shows that the observed decline in *Gilia* population growth from 2004 to 2005 is close to what would be predicted by the 2004–05 change in germination rate alone (holding F at its 3-year average). By contrast, the 2005–06 increase in population growth is consistent with the observed change in the seeds produced per germinant. Consistent with the relatively small change in germination rate across years for *Malacothrix*

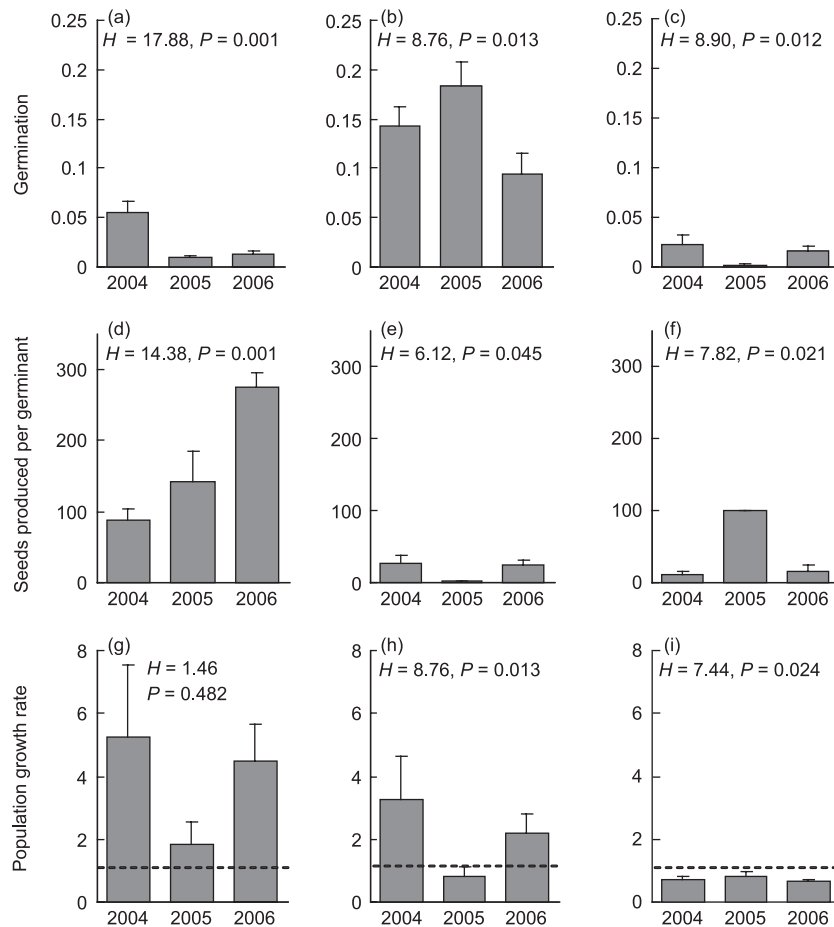


Fig. 5. (a–c) Germination, (d–f) seeds produced per germinant, and (g–i) population growth rate estimates (eqn 2) over 3 years for *Gilia tenuiflora* ssp. *hoffmannii* (column 1) *Malacothrix indecora* (column 2) and *Phacelia insularis* var. *insularis* (column 3). Bars show means ± 1 SE. Presented in each panel is the Kruskal–Wallis test statistic, H , corrected for ties, and the corresponding P -value (d.f. = 2 for all comparisons). The dashed line in (g–i), shows a growth rate of one. In (f), 2005 *Phacelia* survivorship is based on only two germinants, and thus this value should be treated with caution. The corresponding growth rate (i), however, is largely insensitive to changes in germinant survival due to the low germination rate in 2005.

Table 1. Elasticity of the per capita population growth rate, λ , to the germination rate, g , the seeds produced per germinant, F , and the annual survival of seeds in the soil, s , for the three focal annual plants over 3 years

| | 2004 | 2005 | 2006 |
|---|-------|-------|-------|
| <i>Gilia tenuiflora</i> ssp. <i>hoffmannii</i> | | | |
| g | 0.865 | 0.633 | 0.824 |
| F | 0.873 | 0.636 | 0.826 |
| s | 0.126 | 0.363 | 0.173 |
| <i>Malacothrix indecora</i> | | | |
| g | 0.868 | 0.152 | 0.793 |
| F | 0.886 | 0.308 | 0.812 |
| s | 0.113 | 0.691 | 0.187 |
| <i>Phacelia insularis</i> var. <i>insularis</i> | | | |
| g | 0.287 | 0.212 | 0.285 |
| F | 0.303 | 0.213 | 0.296 |
| s | 0.696 | 0.786 | 0.703 |

(Fig. 5b), life table response experiments for this species (Fig. 6b) suggested that variation in the seeds produced per germinant drove its temporal variation in population growth rate. Lastly, variation in *Phacelia*'s population growth rate is related to temporal variation in both the germination rate and the seeds produced per germinant (Fig. 6c). Note that while

the life table response experiments help identify which demographic variable is changing to drive variation in population growth, whether those variables are changing in response to rainfall is a separate question.

RELATIONSHIP BETWEEN POPULATION GROWTH RATES AND ABOVE-GROUND POPULATION DYNAMICS

For all three species, between-year variation in population growth rates incorporating both above- and below-ground dynamics (Fig. 5g–i) was only weakly related to variation in the above-ground plant densities observed in natural populations (Figs 2–4). Even though population censuses showed four times the density of *Gilia* in 2004 vs. 2006 (Fig. 2a), reflecting higher 2004 germination (Fig. 5a), population growth rate estimates were similar due to more seeds produced per germinant in 2006 (Fig. 5g). *Malacothrix* also showed a weak correspondence between its 2004–06 density and population growth rates. *Phacelia*'s population growth rates were less variable than those of the other two species, and were uniformly negative. The consistency of these growth rates contrasted markedly with the near 100-fold variation in the number of germinated plants over the same 3-year period.

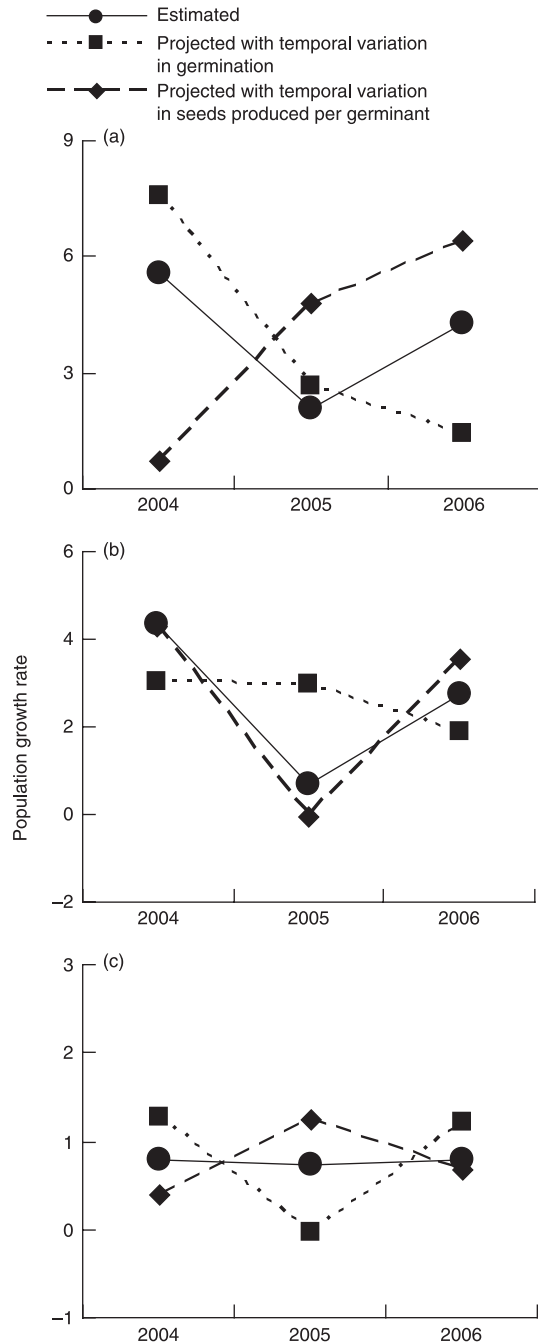


Fig. 6. Life table response experiments for (a) *Gilia tenuiflora* ssp. *hoffmannii*, (b) *Malacothrix indecora* and (c) *Phacelia insularis* var. *insularis*. The solid line shows the estimated population growth rate variation among years. The shorter dash line shows the predicted population growth rate if the germination rate were the only parameter varying between years; the seeds produced per germinant is held at its 3-year average. The longer dash line shows the predicted population growth rate if the seeds produced per germinant were the only parameter varying between years; germination is held at its 3-year average. Each year's population growth rate is calculated from the plot averaged g and F . By contrast, in Fig. 5, growth rates were calculated on a per plot basis then averaged, leading to minor differences between the figures.

Discussion

Understanding the climate factors that drive temporal variation in plant populations is critical to forecasting their persistence under natural and anthropogenically altered climate regimes. The three rare and endangered annual plants of Santa Rosa Island studied here may be particularly threatened by climate change because their geographic ranges are narrow and therefore unlikely to include locations with comparable climates in the future. Indeed, the sensitivity of *Gilia*, *Malacothrix* and *Phacelia* to climate was borne out in the current study. Through years differing greatly in total annual rainfall, and conditions surrounding the first major rainfall event, all three species showed large between-year variation in above-ground springtime plant density (Figs 2–4). For *Phacelia*, this variation was roughly 100-fold and for *Gilia* and *Malacothrix* it was ninefold. Similarly large temporal variation in plant abundance has been noted in a wide range of annual systems, and particularly those of arid and semi-arid regions of the world (Talbot *et al.* 1939; Went 1948; Heady *et al.* 1958; Beatley 1974; Young *et al.* 1981; Bowers 1987; Gutierrez & Meserve 2003; Fox *et al.* 2006).

INTERACTIVE EFFECTS OF WATER LIMITATION AND GERMINATION CUEING ON SPRINGTIME PLANT ABUNDANCE

Temporal variation in rainfall can influence annual plant population dynamics by differentially provisioning water resources across years, differentially cueing germination, or by altering competitive environments. For all species in the current study, low plant abundance during the severe drought year of 2007 supported the water limitation mechanism. However, beyond the effects of severe drought, plant populations seemed remarkably insensitive to season-long rainfall. Species derived little benefit from above average rainfall, as evidenced by low abundance of *Malacothrix* and *Phacelia* plants in the wet 2005 El Niño year, and the only marginally above average *Gilia* plant density that year. In sum, results suggest that droughts force low plant abundance for the three focal species. But there remains considerable variation in plant density in non-drought years, variation that is largely unrelated to total annual rainfall.

Our results support the importance of temperature-based germination cues as a control over the dynamics of our focal annuals in non-drought years. Outside of the 2007 drought year, the nightly low temperature after the first major rain event explained over half the between-year variation in *Gilia* plant density (Fig. 2c), and over 90% of the variation in our significantly shorter time series for *Malacothrix* and *Phacelia* (Figs 3c, 4c). Temperature at the time of seed wetting is well-known to influence the germination of California annuals in general (Went 1949), and in laboratory trials, cold temperatures induce the germination of our three focal species (J.M. Levine, unpublished data). Indeed, the *Gilia* germination rate in the field (Fig. 5a) was highest in the year with the coldest of the germination-inducing storms. In general, these results

suggest that variation in germination is likely to explain much of the between-year variation in plant density in non-drought years.

THE ROLE OF COMPETITOR DYNAMICS AND THE STORAGE EFFECT

Temporal variation in the springtime plant densities of *Gilia* and *Phacelia* was not correlated with the total vegetative cover of their respective surrounding communities. This suggests that between-year variation in competitive suppression is not the major driver of the observed population fluctuations of these two species. Moreover, that they and their competitors respond differently to the environment is a key requirement for positive effects of climate variation on persistence via the storage effect (Chesson 2000). The more differently the rare focal annuals and their competitors respond to different years, the more the competitor species collectively suppress themselves, favouring the persistence of the rare annuals. In contrast to *Gilia* and *Phacelia*, *Malacothrix* showed a non-significant, but negative correlation between its emergent density and cover in the surrounding community. This could reflect the impact of temporal variation in competitive suppression, or alternatively, strong differences in how *Malacothrix* and its competitors respond to different year types.

MECHANISMS UNDERLYING VARIATION IN POPULATION GROWTH RATE

Like springtime above-ground plant density, species per capita growth rate estimates from 2004 to 2006 showed a lack of dependence on season-long rainfall. Growth rates were lowest during the wet 2005 El Niño year for *Gilia* and *Malacothrix*, and negative for *Phacelia* (Fig. 5g–i). Even the seeds produced per germinant, F , the demographic variable which would seem most sensitive to water limitation, was unrelated to season-long precipitation (the high 2005 *Phacelia* value is based on only two germinants). Thus, while elasticity analyses show that F is as important as the germination rate, g , in determining population growth rate of the three focal species, F simply did not correlate with rainfall over the short time series of our study. Similarly, life table response experiments showed that observed variation in F was responsible for much of the observed variation in population growth rate for all three species. However, without a connection between rainfall and F , this result provides little support for the water limitation mechanism.

Elasticity analyses and life table response experiments indicate the variation in g has the same potential as F to drive variation in population growth rates. Indeed, the reduction in *Gilia* population growth rate from 2004 to 2005 could be explained by lower germination in 2005 (Fig. 6a). Importantly, the reduced 2005 germination (Fig. 5a) occurred in a year with warmer first rains (Fig. 1b), providing a link between population growth rate and germination cueing. More generally, based on the high elasticity of g , and its apparent sensitivity to the temperature and the time of the first major rains (Figs 2c, 3c and 4c), we hypothesize that

germination cueing is a key driver of temporal variation in population growth rate.

RELATIONSHIP BETWEEN POPULATION GROWTH RATE AND TRENDS IN SPRINGTIME PLANT DENSITY

A finding with broad implications is that fluctuations in population growth rates were only weakly related to variation in above-ground plant abundance. Most studies of temporal variation in annual plant systems focus on above-ground measures of population performance (Talbot *et al.* 1939; Heady 1958; Beatley 1974; Bowers 1987). Although this likely reflects the ease of obtaining plant density or abundance data, such measures can be misleading when predicting the effects of individual years on population viability. Over longer time scales, however, population growth rates and trends in the above-ground population dynamics should be concordant.

In our study, population growth rate estimates for our three species were generally consistent with decadal long trends in their spring-time population size. *Phacelia* had negative per capita growth rates projected in all 3 years of the study (Fig. 5i), matching long-term trends. In 1998, 1465 plants were noted in the swale and crest sites. Seven hundred and seventy-one plants were counted in these sites in 2001, 360 in 2003 and 21 in 2007. Although low population densities were also observed throughout this time series, peak population sizes over the last 10 years appear to be declining, consistent with the negative growth rates projected here. By contrast, *Malacothrix* and *Gilia*, with much higher projected population growth rates (Fig. 5g,h) have not suffered the decadal decline seen in the *Phacelia* population.

EVOLUTIONARY AND BIOGEOGRAPHIC IMPLICATIONS

One of the most striking results of this study is that all three annuals had their greatest population sizes in years with cold first rains. Although we speculate, this consistency suggests an adaptive explanation may be involved. Indeed, a cold requirement for germination may allow these species to avoid germination with the rare late summer storms (August and September). In coastal California, with its Mediterranean climate, these late summer storms are unlikely to be followed by considerable rainfall for several warm months. This creates drought conditions even more severe than in 2007, when populations were uniformly low. Importantly, the early season storms are usually tropical in origin, and are thus associated with relatively warm weather systems. As a consequence, cold temperatures at the time of seed wetting may be indicative of winter or late fall, a time when subsequent rainfall is almost guaranteed.

Alternatively, cold temperature requirements for germination may be a relictual trait, having evolved in desert environments. Much of the annual plant species diversity in coastal California, including the *Phacelia*, *Gilia* and *Malacothrix* genera, is derived from taxa that historically moved into the region from Mexico via desert environments (Raven & Axelrod 1978). Classic work by Went (1949) has shown that

California winter annuals in the desert require relatively cold temperatures at the time of seed wetting to induce germination (see also Baskin & Baskin 2001). As in the current study, research in desert systems has shown an overriding importance of germination cueing over water limitation in controlling temporal variation in annual plant populations (Went 1949; Beatley 1974; Bowers 1987). High rainfall years only drive large populations of Mojave desert winter annuals if the appropriate germination cues were presented in the fall or early winter (Beatley 1974).

POPULATION PERSISTENCE UNDER CURRENT AND FUTURE CLIMATE REGIMES

Gilia, *Malacothrix* and *Phacelia* showed precipitous declines in springtime plant density over the five focal years of our study (2003–07). Based on our understanding of how rainfall variability affects these populations, their recent declines may not necessarily reflect long-term directional change in population health. Our results lead us to hypothesize that the species were relatively abundant in the early part of the time series (2003 and 2004) because cold first rains were coupled with reasonable subsequent rainfall. Populations were low in 2005 and 2006 because of warm first rains, and low in 2007 because of severe drought conditions. Given that all of these plants have modest to high annual survival of ungerminated seeds (0.57–0.75), a year with cold first rains and non-drought conditions may facilitate their return to higher plant abundance. More generally, these hypotheses emphasize the value of understanding the climatic controls over temporal variation in plant demography when forecasting population persistence and interpreting trends in population dynamics.

Temperature is forecast to increase over the next century in California and elsewhere, while future precipitation regimes are more uncertain (Bell *et al.* 2004; Salinger 2005). Our work suggests that barring severe droughts, changes in the timing and temperatures associated with the first major rains may have much stronger effects on population persistence than changes in total annual rainfall. Even if season-long precipitation remains unchanged, warmer first rains will likely mean lower germination, and lower population growth rates for all three Santa Rosa Island annuals. Our work adds to a growing body of work (Visser & Both 2005) suggesting that alteration of environmental cues may strongly determine how climate change affects plant communities.

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